Modelling wildlife–human relationships for social species with mixed-effects resource selection models

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Summary

1. Resource selection functions (RSF) have contributed to the conservation of species negatively affected by human activities. Despite these applications, two assumptions frequent many studies: the assumption of independence among groups in social species, and that selection is proportional to resource availability. This latter case is known as a functional response in resource selection, and may be especially important in human–wildlife relationships where there is a fitness cost of proximity to humans.

2. Recent advances in generalized linear mixed models offer new ways to account for resource selection in social species and functional responses by accommodating correlations within hierarchical groups with random intercepts, and functional responses with random coefficients.

3. We illustrate the application of mixed-effects RSF models using a case study of resource selection by individual wolves *Canis lupus* living in packs as a function of human activity.

4. In areas of low human activity, wolf resource selection was independent of proximity to humans. As human activity increased, wolves displayed a functional response selecting areas closer to human activity. With increasing human activity, however, wolves displayed spatio-temporal avoidance of human activity during daylight. This could lead to behaviourally induced trophic cascades mediated by wolf avoidance of human activity, and fits within the framework of attractive sink habitats.

5. Accounting for the hierarchical social structure of wolves clearly showed that the response of wolves to human disturbance was strongly correlated, but different, within packs, and that the correlation was strongest during winter and weakest during summer.

6. *Syntheses and applications*. Failure to consider the social structure of wolves and the functional response to human activity would result in mistaken conclusions about wolf–human relationships. Our approach provides a unifying framework to understand the contradictory results of previous studies of wolf–human relationships and a template for future studies to evaluate effects of increasing human activity on wildlife.

Key-words: generalized linear mixed model, hierarchical model, logistic regression, resource selection, wolf

Introduction

Increasing human activity poses a significant threat to wildlife conservation through direct human-caused mortality or indirect causes such as habitat fragmentation and avoidance of human activity (Sinclair & Byrom 2006). The importance of the indirect avoidance of human activity by wildlife is often underappreciated. Wildlife species must make trade-offs between selecting habitats that offer forage resources or avoiding predation risk and/or human activity (Gill, Sutherland & Watkinson 1996; Gill & Sutherland 2000) where human activity is associated with increased mortality (Frid & Dill 2002). Avoidance of areas because of human activity can often have demographically costly consequences (Johnson *et al*. 2004; McLoughlin, Dunford & Boutin 2005). While advances in the study of resource selection have provided new tools to understand wildlife–human relationships (Boyce & McDonald 1999), a persistent difficulty remains unsolved – how to accommodate wildlife responses to gradients in human activity (Mysterud & Ims 1998; Beale & Monaghan 2004). Moreover, many species are social, and responses of

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group-living species to human activity are likely to be correlated within groups, another oft-overlooked problem in wildlife–human relationships. Providing a new statistical approach to remedy these problems for a carnivore species of broad conservation concern is the goal of this study.

Ecologists often examine wildlife–human relationships using resource selection studies to provide guidelines for conservation (Mladenoff *et al*. 1995; Carroll, Noss & Paquet 2001; Johnson *et al*. 2005). Resource selection is usually evaluated by comparing habitats that are used with those that are unused or available using a variety of methods including compositional analysis (Aebischer, Robertson & Kenward 1993), discrete choice models (Cooper & Millspaugh 1999), or the more flexible suite of models known as resource selection functions (RSF) based on logistic regression-based approaches (RSF; Boyce & McDonald 1999; Manly *et al*. 2002). Statistical advances in RSF models especially have overcome earlier methodological deficiencies (Garshelis 2000) by accommodating categorical and continuous covariates, nonlinear functions, autocorrelation (Nielsen *et al*. 2002), and flexible definitions of availability (Compton, Rhymer & McCollough 2002) in multiscale designs that reflect the hierarchical process of habitat selection (Johnson 1980).

There are two difficult-to-remedy RSF model assumptions that remain especially important to wildlife–human relationships. First, few studies acknowledge that resource selection may be more similar among individuals in social groups (e.g. herds) or with geographic areas (e.g. watersheds). Second, previous studies of wildlife–human relationships often assumed a constant response of wildlife to human activity (Mladenoff *et al*. 1995; Carroll *et al*. 2001; Johnson *et al*. 2005). This implicitly assumes that use of a habitat is proportional to the amount of that habitat available – namely that selection is a constant function of availability (Mysterud & Ims 1998). For example, Mysterud & Ims (1998) showed that grey squirrels *Sciurus carolinensis* only selected croplands when they constituted less than 10% of available habitats. They then developed a simple method to model functional responses in a simple two-habitat system that was applied in studies of polar bears *Ursus maritimus* and moose *Alces alces* (Mauritzen *et al*. 2003; Osko *et al*. 2004). Unfortunately, the approach of Mysterud & Ims (1998) cannot be used where there are more than two categorical habitat types, with continuous covariates, in the presence of interactions, or in logistic regression-based RSF designs. Their approach also assumed independence between observations between individual animals or groups. Despite these methodological difficulties, functional responses are expected to be especially important when there is a trade-off in selection for a particular resource, such as where human activity imposes increased risk of mortality (Mysterud & Ims 1998; Frid & Dill 2002). Applied ecologists need more flexible statistical approaches to model functional responses in resource selection, especially for wildlife–human relationships.

Consider the general case when the availability of a habitat covariate in an animal's home range varies such that selection for that covariate varies among individuals, and individuals occur in correlated groups. One class of statistical models that

has been developed to accommodate hierarchically structured responses is that of random effects models (Breslow & Clayton 1993). Recent advances in generalized linear mixed models (GLMMs; mixed because they contain random and fixed effects) can accommodate variable availability and selection within logit models (Skrondal & Rabe-Hesketh 2004) and hierarchically structured data, such as observations within individuals within groups. While the use of random effects models is growing in ecology (e.g. Steele & Hogg 2003; Boyce, Irwin & Barker 2005), we know of only two studies that apply these models to habitat selection. Gillies *et al*. (2006) showed that random intercepts accounted for unbalanced sampling design and correlation among telemetry observations of grizzly bears *Ursus arctos*, dramatically improving model fit and ecological insights. Using simulated data, Gillies *et al*. (2006) suggested functional responses could be accommodated with mixed-effects models. Thomas, Johnson & Griffith (2006) also developed hierarchical Bayesian mixed-effects resource selection models for caribou *Rangifer tarandus*. We know of no empirical studies, however, that use mixed-effects models for functional responses in resource selection, nor resource selection of social species.

The objective of our study was to extend the application of mixed-effect RSFs developed by Gillies *et al*. (2006) to a more complex example of conservation concern involving resource selection by grey wolves *Canis lupus*. Wolves are particularly suited to the use of mixed-effects models to study resource selection for two reasons. First, because they are a social species living within packs, resource selection by individual wolves within a pack may be expected to be more similar within than between packs, suggesting a need for a multi-level hierarchical model (e.g. Begg & Parides 2003). Second, wolves have demonstrated wide variation in response to human activity related to previous persecution by humans (Musiani & Paquet 2004). Thus, a strong trade-off might be expected to occur between selecting habitats close to human activity and wolf survival, suggesting selection should change as a function of the amount of human activity (Mysterud & Ims 1998). We therefore hypothesized that wolves would show a functional response in resource selection to human activity levels. Wolf responses to human activity may be expected to differ seasonally or diurnally (Theuerkauf *et al*. 2003), so we also modelled wolf resource selection separately by season and during night and day.

Materials and methods

STUDY SITE

The study area is located on the eastern slopes the Canadian Rockies in Banff National Park (BNP, 51°30″N, 115°30″W) in Alberta in a 7000-km² area. The study occurred between 15 April 2002 and 15 October 2004. Human activity was concentrated in the Bow valley and Ya Ha Tinda portions of the study area, and was lowest in backcountry areas (Jevons 2001). Human-caused mortality was higher for wolves straddling or outside the boundaries of BNP than those within BNP, and during this study, 100% of radiocollared wolf mortality was caused by trapping (73%) and hunting (27%)

(M. Hebblewhite, unpublished data). On provincial lands, wolves are legally harvested ~9 months of the year, and often illegally during the other 3 months. More details of the study area can be found in Hebblewhite & Merrill (2007).

WOLF TELEMETRY DATA

We modelled resource selection for five wolf packs: the Bow Valley (BV), Cascade (CA), Ranch (RA), Red Deer (RD), and Wildhorse (WH) packs. Wolves were captured using modified foot-hold traps during summer and via helicopter netgunning during winter (University of Alberta animal care protocol no. 353112; Parks Canada MOU no. BNP-01-0064). We fitted wolves with GPS radiocollars (GPS3300sw, LOTEK Ltd, Aurora, Ontario) that were programmed with a 2-h relocation schedule. Fifty per cent of all locations were < 34 m, and 95% < 113 m (Hebblewhite 2006), and we ignored habitat-induced GPS-bias because bias was < 10% (Hebblewhite, Percy & Merrill 2007). We defined two wolf-based seasons: summer (15 April–14 October) and winter (15 October–14 April). We designated locations as day or night based on averaged monthly sunrise and sunset tables (http://www.hia-iha.nrc-cnrc.gc.ca/).

INCORPORATING RANDOM-EFFECTS IN RESOURCE SELECTION FUNCTIONS

We built random effects into the used-availability RSF design (Manly *et al.* 2002) following Gillies *et al.* (2006), wherein resource covariates are compared at used and available locations using:

$$\hat{w}(x) = \exp(\mathbf{X\beta}) \qquad \text{eqn 1}$$

where $\hat{w}(x)$ is the relative probability of use as a function of covariates x_n, and $\mathbf{X\beta}$ is the vector of the fixed-effect resource selection coefficients $\hat{\beta}_1 x_1 + \hat{\beta}_2 x_2 + ... + \hat{\beta}_n x_n$ estimated from fixed-effects logistic regression (Manly *et al.* 2002). The RSF is a relative probability function, not a true probability function (i.e. a RSPF), because use is compared with available locations (Manly *et al.* 2002). For this analysis, we considered wolf selection within the home-range, or at the third order scale following Johnson's (1980) hierarchy of scales of selection. We chose this spatial scale because previous analyses showed little variation at the second order scale of where wolves select territories within the study area (M. Hebblewhite, unpublished data). Therefore, availability of covariates was measured at the pack level using one random location per square kilometre of seasonal territory size, estimated from the 99th percentile kernel territory boundary (Hebblewhite 2006). Random dates and times were calculated for available points to designate points as day or night. The same random points were used for each wolf within each pack to keep availability constant within packs. For comparison with mixed-effects models, we estimated fixed-effects RSF models using equation 1 and call this the naïve RSF hereafter.

Building on equation 1, random intercepts were included to accommodate the hierarchical structure of wolves within packs via a mixed-effects GLMM with the logit link (Skrondal & Rabe-Hesketh 2004). Next, we added a random coefficient for proximity to high human use (see Habitat covariates section below) to test for the functional response to human activity. The form for a generalized three-level mixed-effects model for location *i*, wolf *j*, and pack *k*, with a random coefficient, is:

$$\text{Logit}(y_{ijk}) = \beta_0 + \gamma_{jk}^{(wolf)} + \gamma_k^{(pack)} + \gamma_{1jk}^{(wolf)} x_{ijk}$$
$$+ \gamma_{1k}^{(pack)} x_{ijk} + ... + \mathbf{X\beta} + \varepsilon_{ijk} \qquad \text{eqn 2}$$

where β_0 is the fixed-effect intercept, $\gamma_{jk}^{(wolf)}$ and $\gamma_k^{(pack)}$ are the random variation in the intercept at the wolf and pack levels, $\gamma_{1jk}^{(wolf)} x_{ijk}$ is the variance around β_1 among individuals (wolf-level) for covariate x_{ijk}, $\gamma_{1k}^{(pack)} x_{ijk}$ is the variance around β_1 arising from variation among packs (pack-level) for covariate x_{ijk}, $\mathbf{X\beta}$ is the vector of the fixed-effect resource selection coefficients for covariate x_{ijk} (equation 1), and ε_{ijk} is unexplained residual variation. Our notation for random effects follows Rabe-Hesketh & Skrondal (2005, p. 236) and Gillies *et al.* (2006). Note in equation 2 that the full model has random coefficients for both *j* and *k*, but at present, only one random coefficient can be accommodated in statistical packages (Rabe-Hesketh & Skrondal 2005). Thus, we only consider models that allow coefficient variation in *j* only or *k*. We use model fit and random effect size to determine at which level (wolf, pack) the random coefficient for human activity occurs (see model selection below).

Mixed-effect logit models were estimated with STATA 8·0 (StataCorp 2003) using GLLAMM (www.gllamm.org; sample STATA code is given in Appendix S1, Supplementary material). GLMMs can also be estimated using other packages such as SAS (PROC GLIMMIX, http://support.sas.com/rnd/app/papers/glimmix.pdf), S-Plus, R (using glme and glmmPQL, and glmmML, glmm, respectively, Pinheiro & Bates 2000), and hierarchical Bayesian approaches such as winBUGS (e.g. Thomas *et al.* 2006). We opted to use the GLMM approach using STATA 8·0 rather than a Bayesian winBUGS approach because of relative conceptual ease for ecologists familiar with generalized linear models (GLM), and (at the time) because of computational (convergence) difficulties with large GPS location data sets in winBUGS. We derived maximum-likelihood estimates (MLEs) in GLLAMM using adaptive quadrature (Rabe-Hesketh, Skrondal & Pickles 2005) with 12 integration points. Computation time is presently a limiting factor for any GLMM approach (STATA, R, SAS); several of the models took > 2 days to converge, but advances in computational power and multiple-processing will continue to improve efficiency. Our mixed-effect RSF models made the following assumptions: (i) correlations within wolves and packs were constant (see below), (ii) correlations between wolves and packs were constant, and (iii) random effects were normally distributed with a zero mean and unknown variance components (Breslow & Clayton 1993; Skrondal & Rabe-Hesketh 2004). We discuss the first two assumptions below, and tested the assumption of normality for the distribution of random coefficients at the wolf level ($n = 15$) because a meaningful test with $n = 5$ packs could not be conducted. While GLMMs are often robust to violation of this assumption, Skrondal & Rabe-Hesketh (2004) provide information on how to include non-normal random effects in GLMMs.

A distinct advantage of mixed-effects models is the ability to provide both *marginal* and *conditional* inferences (Breslow & Clayton 1993; Skrondal & Rabe-Hesketh 2004). The *marginal* or *population*-level RSF model corresponds to the mean resource selection patterns averaged across the hierarchically structured wolf population. For *population-level* inference, the fixed-effects estimates from equation 2 are applied to equation 1 akin to typical RSF models (Manly *et al.* 2002) following:

$$\hat{w}(x) = \beta_1 x_{ijk} + \beta_2 x_{ijk} + ... + \mathbf{X\beta} \qquad \text{eqn 3}$$

where equation 3 is a reduced form of equation 2 with no random intercepts nor coefficients. We note that, although the intercept is dropped by convention from equation 1 in RSF models (Manly *et al.* 2002), including a random intercept changes the β coefficients (Breslow & Clayton 1993).

Conditional inferences are evaluated for either the individual wolf, *j*, or individual pack, *k*. In this paper we focus on *pack-level* conditional inferences, but direct readers to Appendix S2 in the Supplementary material where wolf-level inferences are presented for comparison. For *pack-level* inferences, equation 2 is solved using conditional estimates for a specific pack, e.g. *k* = 1 following:

$$\hat{w}_k(x) = \gamma_k^{(pack)} + \gamma_{1k}^{(pack)} x_{ijk} + ... + \mathbf{X\beta} \qquad \text{eqn 4}$$

Note equation 4 is a reduced form of equation 2 for just pack-level (not wolf-level) responses.

CORRELATION WITHIN AND BETWEEN GROUP-LEVELS

For three-level mixed-effects models, one can also estimate the: (i) within pack correlation, (ii) correlation between wolves in a specific pack, and (iii) correlation between locations within a pack holding the effects of wolf constant (following Rabe-Hesketh & Skrondal 2005). This helps address assumptions about intra- and inter-pack correlations, and also identifies the greatest source of variation and how best to incorporate random effects into the model.

For the same wolf pack *k*, but different wolves *j* and *j'*, the *within-pack correlation* is:

$$\rho(pack) = Cor(y_{ijk}, y_{i'j'k} \mid x_j x_{j'}) = \frac{\psi^{(pack)}}{\psi^{(wolf)} + \psi^{(pack)} + \frac{\pi}{3}} \qquad \text{eqn 5}$$

where $\psi^{(pack)}$ is the variance at the pack level, $\psi^{(wolf)}$ is the variance at the level of wolf, and $\pi/3$ is the variance in ε_{ijk} (given a logit model). For the same individual wolf *j* within pack *k*, the *within-wolf correlation* is:

$$\rho(wolf, pack) = Cor(y_{ijk}, y_{i'jk} \mid x_j) = \frac{\psi^{(wolf)} + \psi^{(pack)}}{\psi^{(wolf)} + \psi^{(pack)} + \frac{\pi}{3}} \qquad \text{eqn 6}$$

and finally, considering the correlation between locations in the same pack for a given individual wolf

$$\rho(pack \mid wolf) = Cor(y_{ijk}, y_{i'jk} \mid j) = \frac{\psi^{(pack)}}{\psi^{(pack)} + \frac{\pi}{3}} \qquad \text{eqn 7}$$

which can be thought of as a measure of how consistent resource selection is at the individual wolf level. In all cases, the numerator is the variance shared between both levels, and the denominator is the total variance for equations 5 and 6, but without the variance due to individual wolf in equation 7 because the effect of wolf is held constant. In a proper three-level random effects model, the variances of the random intercepts are positive > 0, and variance decomposes such that $\rho(wolf, pack) > \rho(pack)$. This is because telemetry locations within a wolf are more similar than between different wolves within the same wolf pack.

MODEL SELECTION

Model selection was conducted hierarchically (*sensu* Ten Have, Kunselman & Tran 1999). First, we used AIC$_c$ (Burnham & Anderson 1998) to identify the covariates of the top fixed-effect model (equation 1) with their interactions from an a priori candidate model list. Second, the top mixed-effect model structure was

selected using AIC$_c$ by adding to the top-fixed effects: (i) a random intercept for wolf, (ii) a random intercept for pack, (iii) a random intercept for wolf and pack, (iv) two random intercepts and a random coefficient for packs, and (v) same as (iv) but substituting a random coefficient for wolf rather than pack The number of parameters *k* was calculated as for fixed-effects models, plus one for each random intercept, and two for each random coefficient for the variance and covariance (Skrondal & Rabe-Hesketh 2004). We used conventional AIC$_c$ for model selection because we were interested in inferences to the population of wolf packs. For conditional inferences within only a pack/wolf, conditional AIC, or cAIC, is recommended by Vaida & Blanchard (2005).

HABITAT COVARIATES

We considered the following six GIS covariates as fixed-effects in wolf RSF models: landcover, elevation, slope, aspect, distance to edge, and proximity to high human activity. Landcover type was described from an existing landcover map for the study area derived from Landsat (see Hebblewhite 2006) collapsed to nine landcover types included as dummy variables: forested (the reference category combined closed and moderate coniferous, mixed, and deciduous types), open conifer, herbaceous, shrubs, deciduous, rock/ice/snow, alpine, recent fires, and regenerating cutblocks. Bergmann *et al.* (2006) found wolves selected areas closer to 'hard' habitat edges. Therefore, we similarly defined 'hard' edges as any edge between open (herbaceous, shrubs, deciduous, rock, alpine, fire) and closed-canopied habitats (forested, open conifer) and between river/stream edges, and calculated distance (km) to these edges. The three topographic variables of elevation (m), slope (%), and aspect-class (north, south, flat) were derived from a 30 m^2 resolution Digital Elevation Model (DEM).

Human activity on linear features influenced movements of wolves elsewhere in the Canadian Rockies (Whittington, St Clair & Mercer 2005). We used the human use digital atlas of the Central Rockies Ecosystem (Jevons 2001) to quantify human activity along all ~6000 km of combined linear features (including roads, trails, and seismic exploration cutlines). Average density of linear features was 0·81 km^{-2}, but varied from > 12 km^{-2} near towns to < 0·5 km/km^{-2} in remote backcountry areas. We used Jevons' (2001) quantitative cut-off of 100 human-use events per month to classify human activity on each linear feature as either high or low. Once classified, proximity to linear features with high human activity was calculated in kilometres. We screened against including collinear variables in RSF models using a *r* = 0·5 as a threshold cut-off value (Hosmer & Lemeshow 2000).

MODELLING THE FUNCTIONAL RESPONSE

We tested for a functional response in wolf use of areas close to high human activity using pack-specific random coefficients, $\gamma_{1k}^{(pack)}$ from equation 4. Each wolf territory's mean proximity to high human activity was measured using zonal statistics++ in Hawth's Analysis Tools 3·19 (Beyer 2005) and ArcGIS 9·0 (ESRI). Then, for each night/day and summer/winter model, we used a logarithmic function (e.g. Mysterud & Ims 1998) to estimate the functional relationship between the estimated random coefficient, $\gamma_{1k}^{(pack)}$ (as a dependent variable), and each territory's mean proximity to high human use, $\bar{x}_k$, the independent variable. This functional response was then used to create maps of the relative probability of use by wolves using the marginal and conditional models.

MAPPING THE FUNCTIONAL RESPONSE

Mapping the marginal (population) RSF was straightforward using GIS covariates and equation 3 for the top model (Manly *et al.* 2002). However, mapping the conditional (pack-level) RSF was problematic because any functional response observed is contingent on the scale of investigation (Mysterud & Ims 1998). Therefore, we used a 16-km radius moving window analysis based on radius of the mean seasonal wolf territory size, 800 km^2 (Hebblewhite 2006) to calculate the average home range scale proximity to high human use, $\bar{x}_k$. The logarithmic functional response between $\gamma_{1k}^{(pack)}$ and $\bar{x}_k$ was then used to create a GIS coverage making $\gamma_{1k}^{(pack)}$ spatially explicit. We then substituted this spatially explicit $\gamma_{1k}^{(pack)}$ as the coefficient for human activity into equation 3 for each landscape cell. Predicted relative probabilities were rescaled between 0 and 1 for both the marginal and conditional maps (Manly *et al.* 2002). All RSF mapping were conducted using ArcGIS 9·2 raster calculator (ESRI Ltd 2004).

Results

We captured and outfitted 16 wolves from the five packs with GPS collars, from which we obtained 17 575 GPS locations, or an average of 541 GPS locations per season per wolf. Inclusion of any random effect, including just a random intercept, dramatically improved fit over the naïve RSF model by hundreds of ΔAIC units (Table 1). For all seasonal and time of day models, the top model was selected unequivocally, and included random intercepts for wolf and pack, and a pack-level random coefficient for proximity to high human use (model $\gamma_{jk}^{(wolf)} + \gamma_{k}^{(pack)} + \gamma_{1jk}^{(pack)} x_{1ijk}$, Table 1). The model with random intercepts for pack and wolf but a random coefficient at the wolf level (model $\gamma_{jk}^{(wolf)} + \gamma_{k}^{(pack)} + \gamma_{1jk}^{(wolf)} x_{1ijk}$,) failed to converge during summer, but did converge during winter, when it was the second-ranked model (Table 1). After the top model, there was considerable variation in model ranking among random intercept and random coefficient models, and whether effects were stronger at the wolf or pack level (Table 1). Comparison of the frequency of normalized individual wolf random coefficients to that expected assuming a normal distribution (Fig. 1) supports the assumption of normality at the individual wolf level (e.g. Steele & Hogg 2003), and by inference, at the wolf pack level.

The habitat covariates influencing resource selection during summer were consistent across seasonal and temporal models. Wolves strongly avoided steeper slopes and strongly selected for areas closer to 'hard' edges (Table 2). Wolves also selected burned and alpine areas during summer, but selected burns less and avoided alpine completely in the winter (Table 2). Avoidance of higher elevations was mirrored by stronger avoidance of rock during winter. Seasonal differences between selection for herbaceous and shrubs were not as different as temporal differences; wolves selected both more at night than day (Table 2). Finally, open conifer and cutblocks were selected during summer, but were as equally avoided as forested habitats during winter (Table 2).

Table 1. Results of model selection for summer and winter mixed-effects resource selection models for wolves during day and night, showing model structure, number of fixed (see Table 2) and random parameters (*k*), log-likelihood (LL), sample size (*n*), and ΔAIC. Model structures are: **Xβ**, fixed effects naïve logit model, $\gamma_{jk}^{(wolf)}$, random intercept for effect of wolf, $\gamma_{k}^{(pack)}$, random intercept for pack, $\gamma_{1jk}^{(wolf)} x_{1ijk}$, random coefficient for distance to high human use for individual wolves, $\gamma_{1jk}^{(pack)} x_{1ijk}$, random coefficient for proximity to high human use for wolf packs. Sample sizes were *n* = 10 294, 7544, 4776, and 5268 for summer day, night, and winter day and night models, respectively. The top selected model is in bold

Model name	Structure	Random *k*	Summer models (fixed *k* = 11)		Winter models (fixed *k* = 9)	
			LL	ΔAIC	LL	ΔAIC
Daytime model						
Naïve fixed effects logit	**Xβ**	0	−4518·4	861·81	−2727·6	1178·9
Random intercept for wolf	$\gamma_{jk}^{(wolf)}$	1	−4181·3	189·64	−2205·1	135·9
Random intercept for pack	$\gamma_{k}^{(pack)}$	1	−4405·2	637·49	−2442·8	611·4
Random intercept for wolf and pack	$\gamma_{jk}^{(wolf)} + \gamma_{k}^{(pack)}$	2	−4181·3	191·53	−2158·9	45·5
Random intercept for wolf, pack, and random coefficient for wolf	$\gamma_{jk}^{(wolf)} + \gamma_{k}^{(pack)} + \gamma_{1jk}^{(wolf)} x_{1ijk}$	4	Failed to converge*		−2143·2	18·2
Random intercept for wolf, pack, and random coefficient for pack	$\gamma_{jk}^{(wolf)} + \gamma_{k}^{(pack)} + \gamma_{1jk}^{(pack)} x_{1ijk}$	**4**	**−4083·5**	**0·00**	**−2134·1**	**0**
Night model						
Naïve fixed effects logit	**Xβ**	0	−3456·1	628·58	−2647·9	1184·5
Random intercept for wolf	$\gamma_{jk}^{(wolf)}$	1	−3251·4	221·19	−2125·1	140·9
Random intercept for pack	$\gamma_{k}^{(pack)}$	1	−3440·8	600·00	−2354·7	600·1
Random intercept for wolf and pack	$\gamma_{jk}^{(wolf)} + \gamma_{k}^{(pack)}$	2	−3252·0	224·28	−2060·3	13·3
Random intercept for wolf, pack, and random coefficient for wolf	$\gamma_{jk}^{(wolf)} + \gamma_{k}^{(pack)} + \gamma_{1jk}^{(wolf)} x_{1ijk}$	4	Failed to converge*		−2053·5	3·7
Random intercept for wolf, pack, and random coefficient for pack	$\gamma_{jk}^{(wolf)} + \gamma_{k}^{(pack)} + \gamma_{1jk}^{(pack)} x_{1ijk}$	**4**	**−3137·9**	**0·00**	**−2051·6**	**0**

*Convergence failure is thought to have occurred because for the same second-ranked winter model (Table 1) ρ(*wolf*, *pack*) < ρ(*pack*) (unpublished data), a biologically nonsensical result (Skrondal and Rabe-Hesketh 2004). See Appendix S2 for more details.

Table 2. Model structure and marginal parameters of the top seasonal (summer, winter) and temporal (night, day) three-level mixed-effects model for resource selection estimated with GPS locations (level 1) with random intercepts for wolf (level 2) and pack levels (level 3), and a random coefficient at the pack level for wolf response to proximity to high human use. *indicates significant at a conservative $P = 0.05$

	Summer RSF model				Winter RSF model			
	Day model		Night model		Day model		Night model	
N – level 1, 2, 3	10294, 11, 5		7544, 11, 5		4776, 13, 5		5268, 13, 5	
Condition no.†	171·5		111·7		139·6		118·3	
Fixed effects	Day	SE-day	Night	SE-night	Day	SE-day	Night	SE-night
Intercept	1·92	0·066*	1·54	0·283*	0·77	0·377*	1·14	0·402
Distance to high human use	–0·15	0·014*	–0·12	0·064	–0·22	0·128	–0·21	0·109
Distance to edge (km)	–1·31	0·120*	–1·52	0·147*	–1·23	0·187*	–1·38	0·204
Slope	–0·08	0·003*	–0·09	0·004*	–0·07	0·005*	–0·11	0·005
Burn	1·37	0·113*	1·13	0·131*	0·24	0·146	0·32	0·142
Alpine	0·53	0·114*	0·13	0·129	–0·48	0·23*	–0·65	0·237
Shrub	0·99	0·131*	1·15	0·140*	0·11	0·147	0·93	0·159
Rock	–0·46	0·089*	–0·46	0·105*	–1·43	0·152*	–0·95	0·171
Oconif	0·52	0·100*	0·38	0·102*	Dropped from final model¶			
Herbaceous	0·54	0·161*	1·40	0·170*	0·72	0·189*	1·29	0·161
Cutblock	0·59	0·285*	1·36	0·390*	Dropped from final model¶			
Random effects	Variances and covariances							
$\gamma_{jk}^{(wolf)}$	0·238	0·023	0·930	0·344	9·200	3·370	9·870	3·660
$\gamma_{k}^{(pack)}$	2·083	0·177	0·343	0·013	1·260	0·603	0·331	0·375
$\gamma_{1jk}^{(pack)} x_{1ijk}$	0·269	0·039	0·085	0·031	0·459	0·296	0·200	0·173
COV‡	0·268	0·041	–0·107	0·058	–0·069	0·072	–0·111	0·086
COR§	0·358	–	–0·622	–	–0·091		–0·433	
Intraclass correlations								
ρ(pack)	0·618		0·148		0·109		0·029	
ρ (wolf, pack)	0·689		0·549		0·909		0·907	
ρ (pack | wolf)	0·665		0·247		0·546		0·240	

†Condition number is an index of how well the model is identified. In binomial models, where model identification is difficult, values less than a few hundred are acceptable (Rabe-Hesketh and Skrondal 2005).
‡COV is the covariance between the random intercept and random coefficient at the pack level.
§COR is the correlation between the random intercept and random coefficient at the pack level.
¶Note these two landcover types were statistically insignificant during winter and were dropped from the final model, grouped with the intercept.
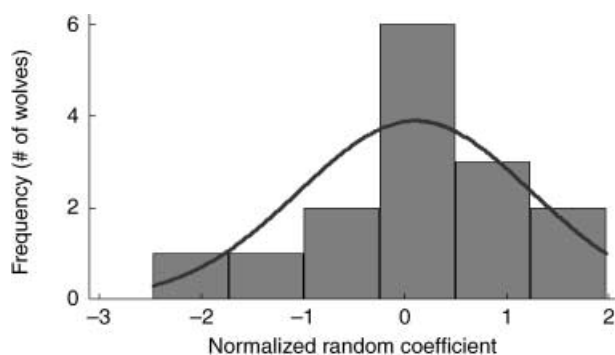

Fig. 1. Frequency distribution of (normalized) random coefficient for individual wolf responses to human activity during daytime. The overlaid curve gives the expected frequency under the assumption that individual coefficients are distributed according to a normal distribution with mean and variance equal to the empirical distribution.

During summer in the day, the correlation between all wolves within packs, ρ(pack), and between wolves for a specific pack, ρ(wolf, pack), were relatively similar, 0·62 and 0·69 respectively. Wolves within packs were less correlated than with other packs at night in summer (0·15 vs. 0·55, respectively; Table 2). This continued during the winter where different packs were not correlated at all during either night or day (ρ = 0·11, 0·03) but when wolves within a specific pack were highly correlated (ρ = 0·909, 0·907). Finally, locations for a given wolf were more correlated during the day during both seasons than at night (Table 2). As theoretically expected, in all cases ρ(wolf, pack) > ρ(pack) (Skrondal & Rabe-Hesketh 2004).

Marginal coefficients in Table 2 account for the hierarchical data structure of wolves within packs, and were vastly different from naïve-logit estimates (Fig. 2, see Hebblewhite 2006 for detailed parameter estimates). The naïve-RSF model showed no selection by wolves to human activity, whereas the marginal coefficient revealed selection of areas close to human activity (Fig. 2). In contrast, pack-level wolf selectivity for proximity to high human use changed dramatically between packs within seasons (Fig. 2). The BV pack always selected areas closer to human activity, as did the RA pack except during daytime in the winter when they selected areas away from human activity, while the WH pack followed an opposite
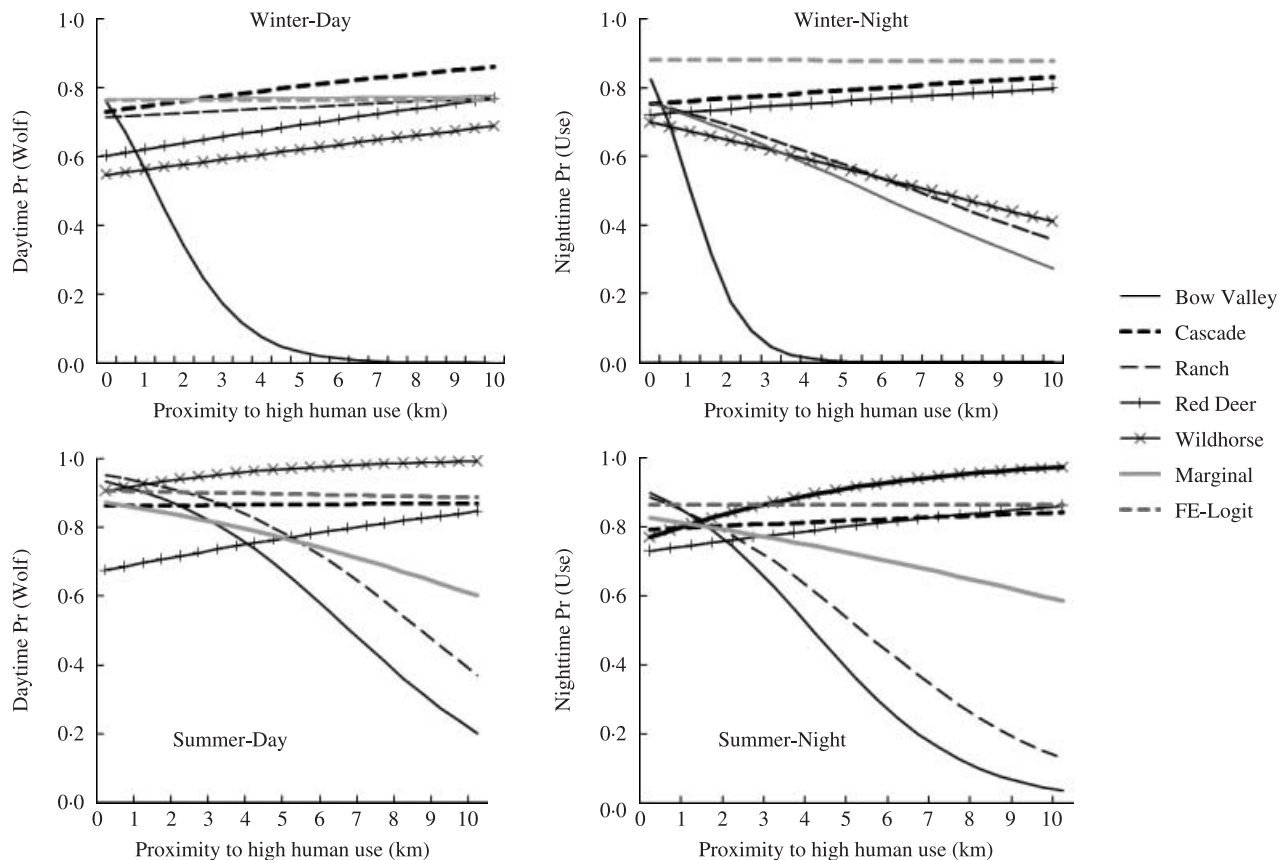
Fig. 2. Conditional relative probabilities of use as a function of proximity to high human use seasonally and temporally for wolves in the eastern slopes of Banff National Park and adjacent areas, 2002–2004. Conditional predictions from three-level (location–wolf–pack) mixed-effects generalized linear mixed-model (GLMM) resource selection function (RSF), and are conditional on the specific pack, holding all other effects constant. The marginal, or population-level prediction, and prediction from the naïve logit, which ignores the hierarchical structure of the data, are shown for comparison.

Table 3. Wolf–human use functional response model parameter estimates between the selectivity coefficient ($\gamma_{1jk}^{(pack)}$) and seasonal wolf home range-scale proximity to high human use (x_{1ijk}). Nonlinear model form $\gamma_{1jk}^{(pack)} = \beta_0 + \beta_1 * \mathrm{Ln}(x_{1ijk})$. Model estimated using nonlinear least squares, and *indicates significant at a conservative $P = 0.10$ because of small sample size

Model	β_1	SE	β_0	SE	$F_{1,4}$	P	R^2-Adj
Summer day	0·2	0·085*	–0·232	0·107*	5·62	0·095	0·54
Summer night	0·291	0·097*	–0·356	0·17*	8·84	0·058	0·66
Winter day	0·295	0·13*	–0·3562	0·17	4·77	0·110	0·45
Winter night	0·49	0·19*	–0·722	0·245*	6·33	0·085	0·57

pattern, selecting areas far from humans except during the day in winter. Finally, both the CA and RD pack consistently selected areas far from human activity (Fig. 2).

Wolf selection for human activity changed across availability and time of day consistent with a functional response in resource selection (Fig. 3, Table 3). As human activity increased within territories, wolves became constrained to select areas close to human activity, whereas packs occupying areas with much lower human activity seemingly ignored human activity (Fig. 3, Table 3). The functional response interacted with time of day such that wolves in high human activity areas moved closer to human activity during night-time, but spatially avoided these areas during the day (Fig. 3, Table 3).

The final mixed-effects model for each season and time of day was used to generate spatial predictions of the population and pack-level wolf RSF, shown in Fig. 4. Inclusion of the random effect clearly illustrates differences between the conditional and marginal models, especially surrounding the Ya Ha Tinda Ranch (Fig. 4), and provides clear support for the biological interpretation of Fig. 2.

Discussion

Including random effects in RSF models provided richer ecological insights into the relationship between wolf resource selection and human activity than fixed-effects models. The
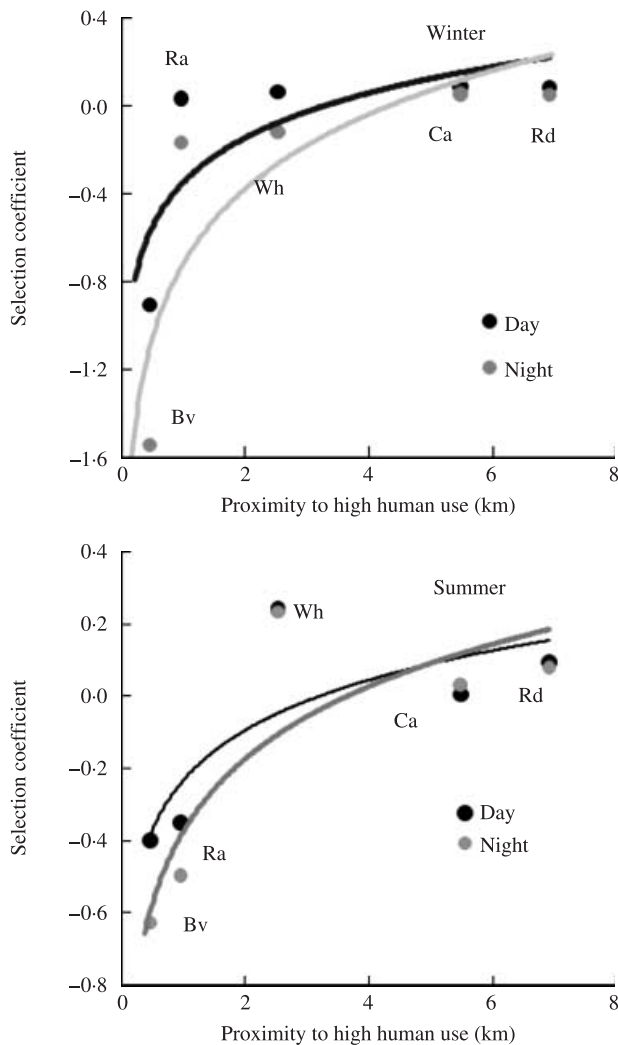
Fig. 3. Functional response in resource selection by wolves as a function of changing seasonal home range proximity to high human use across wolf packs along the eastern slopes of Banff National Park. The functional response of wolves to human activity interacts with time of day only in areas close to high human activity. The available proximity to high human use was calculated at the seasonal home range level during winter and summer. Conditional selection coefficients for wolf packs during day and night periods were estimated from a three-level (location–wolf–pack) mixed-effects generalized linear mixed-model (GLMM) resource selection function (RSF). Acronyms of wolf packs are given in the text.

effects of the fixed-covariates, namely wolf avoidance of steep slopes, selective use of hard edges, and general selection for areas supporting higher ungulate forage biomass, were consistent with previous studies of wolves in mountainous terrain (Whittington *et al.* 2005; Bergmann *et al.* 2006). The real ecological insights of mixed effects come from understanding diurnal variation between and within wolf packs with respect to human activity. Individual wolves responded to human activity more similarly within than between wolf packs. Wolf packs that occurred far from high human activity responded randomly to human activity at all times of the day. As human activity increased, wolf resource selection followed a functional response whereby packs were constrained to select areas closer

to human activity at the home-range scale. At high human activity levels, however, this functional response diverged between night and day, revealing spatio-temporal avoidance of human activity during daytime, when human activity is the highest.

This study also firmly demonstrates that random effects are a fundamental property of the experimental design (Bennington & Thayne 1994) and crucial to model fit. Models without a random intercept were thousands of times less likely to be the best model. Furthermore, without random effects, researchers can really only make valid inferences to the sampled units, not to the population, akin to their interpretation in ANOVA (Bennington & Thayne 1994). Failure to include mixed-effects has undoubtedly hindered previous studies which often pooled and/or discarded data to estimate one fixed-effects logit to reduce autocorrelation (Mladenoff *et al.* 1995). Yet our study demonstrated the limitations of averaging models because the population effects were not equivalent to the pack-level responses or to the naïve logit effects. Thus, estimating one RSF model per pack and averaging coefficients is not necessarily equivalent to the marginal estimate, and would not allow true population-level inferences (Skrondal & Rabe-Hesketh 2004). While random effects may not be useful for some situations, we argue that argue that random effects should be considered as a priori aspects of experimental design for resource selection studies, especially for social species.

Mixed-RSF models will also open research into the consequences of individual behaviour to population dynamics. For example, the wolf (#77) that selected areas closest to human activity (Table S1, Supplementary material) was shot by a human. With enough mortality data, researchers could link resource selection to the fitness consequences (McLoughlin *et al. 2*005). This approach would allow a landscape to be divided into demographic categories according the framework of source-sink dynamics and attractive sinks (Nielsen, Stenhouse & Boyce 2006). For example, given the trade-off between selection for high productivity areas outside the park and areas far from human activity, wolf habitat could be divided into source habitat (e.g. the Red Deer river inside the park), poor-quality habitat (high elevation nonproductive sites), and attractive sinks (e.g. the Ya Ha Tinda ranch, Fig. 4) where productivity and ungulate biomass is high, but where survival is reduced because of human activity (Nielsen *et al.* 2006). Partitioning by age- and sex-class may also provide insight into potential life-history consequences of resource selection (Steele & Hogg 2003). For example, breeding female wolves demonstrated the most 'conservative' (strongest) human avoidance behaviour of all age–sex classes (Table S1, Supplementary material); such insights would not be possible from naïve logistic modelling approaches.

Even a cursory review of previous wolf–human studies supports our interpretation of the overriding importance of wolf functional responses to human activity. Wolves selected seismic lines in the low-human density boreal forests of Alberta (James & Stuart-Smith 2000), avoided paved but selected dirt roads with moderate human activity in Italy (Ciucci, Masi & Boitani 2003), avoided areas of higher human activity during the day in Poland (Theuerkauf *et al.* 2003), and selected to be
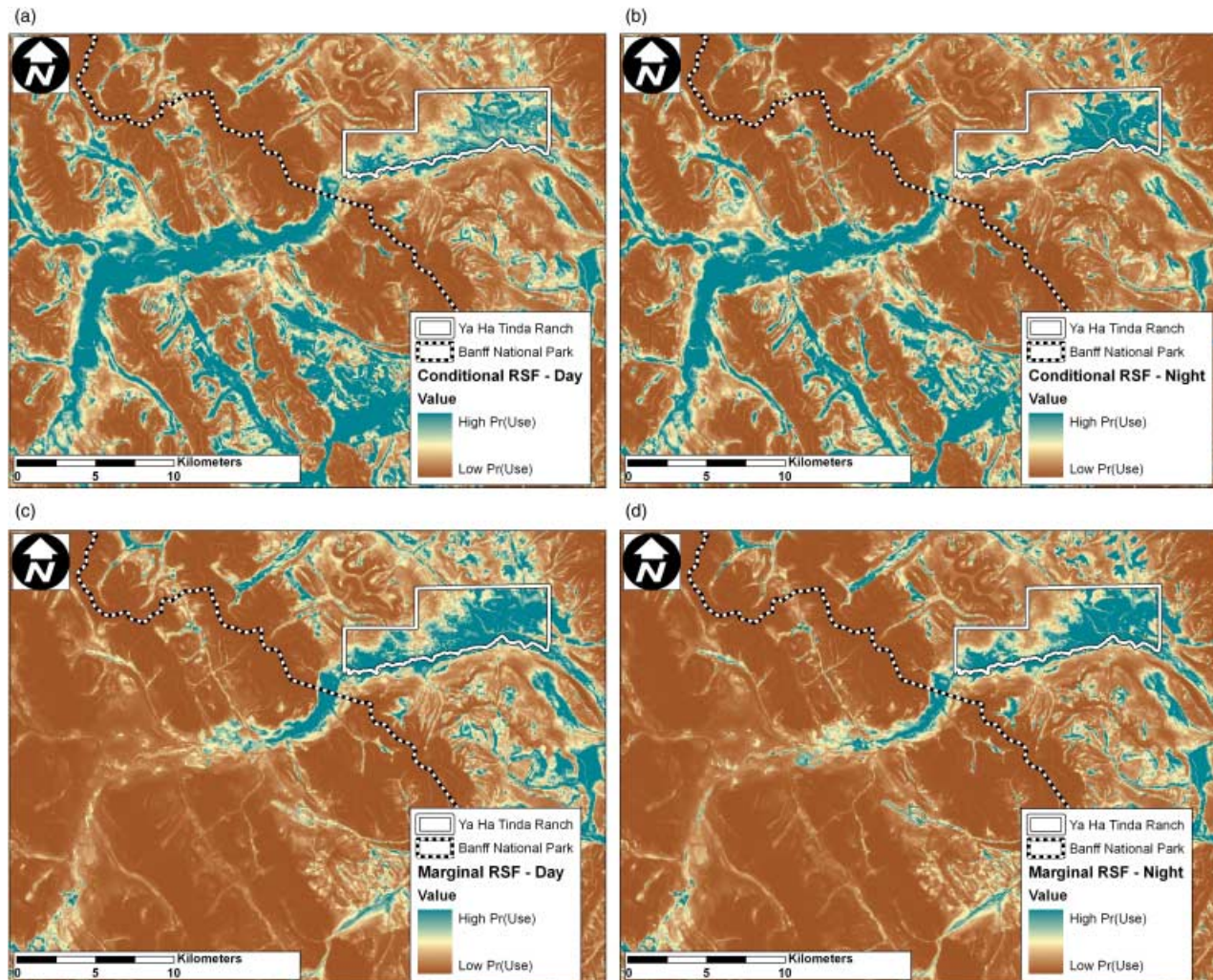
Fig. 4. Comparison of conditional (a and b) and marginal (c and d) inferences from three-level mixed effects wolf RSF models during summer between night (b and d) and day (a and c). Probability of wolf use is scaled between 0 (low) and 1 (high). Ya Ha Tinda (red) outside BNP is characterized by high human activity levels, whereas inside BNP in the Red Deer river is characterized by the lowest human activity levels in the study area. Inferences differ between the marginal and conditional models across this gradient only in areas of high human use at the Ya Ha Tinda ranch during summer via a spatio-temporal refuge from predation.

close to areas of low human activity but far from high human activity areas in the Canadian Rockies (Whittington *et al*. 2005). This variation among studies suggests wolves respond more to the level of human activity rather than density of roads or trails, avoiding human activity only at high levels (Whittington *et al*. 2005). We found quantitative support for this hypothesis as revealed by wolves' functional response to gradients in human activity. Given the evolutionary and recent history of human persecution of wolves by humans (Musiani & Paquet 2004), the functional response of wolves to human activity is surely adaptive. Wolf avoidance of human activity also has important trophic implications because ungulates may increase in areas of high human activity because of reduced wolf use, with resultant trophic cascades to plants (Hebblewhite *et al*. 2005).

Our approach provides a unifying framework to understand the contradictory literature on wolf–human relationships, and a conceptual approach to model wildlife–human relationships for other sensitive wildlife species. Inclusion of a random coefficient in RSF models is advised where individual animals exhibit variable selection for a resource (e.g. Gillies *et al*. 2006), or may be expected to demonstrate a functional response in resource selection for a limiting resource (Mysterud & Ims 1998). Where a functional response does not occur, inclusion of random intercepts is still advisable for improving model fit and estimates, especially for social species. New advances in resource selection modelling make inclusion of mixed-effects models possible in approaches for estimating resource selection probability functions (Lele & Keim 2006) and logistic discriminant functions (Johnson *et al*. 2006). We hope the growing evidence demonstrating clear benefits of modelling resource selection with mixed-effects models will convince ecologists of their utility.

Acknowledgements

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Supplementary material

The following supplementary material is available for this article:

Appendix S1. Sample annotated STATA analysis code for analyzing a three-level generalized linear mixed-RSF models

Appendix S2. Conditional resource selection inferences and functional responses from the top three-level mixed-effects RSF models for the individual wolf level

Table S1. Individual wolf coefficients for proximity to high human activity during night and day, winters 2002/2003 and 2003/2004, eastern slopes of BNP, Alberta, Canada

Fig. S1. Individual wolf functional response in selection as a function of proximity to average human activity at the wolf pack home-range level during night and day, winters 2002–2004.

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